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**Title**

Mass attack by the ambrosia beetle *Platypus quercivorus* occurs in single trees and in groups of trees

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## Abstract

Bark and ambrosia beetles sometimes kill trees by attacking them *en masse*; however, their attack is not necessarily successful. Less than half of the fagaceous trees attacked by the ambrosia beetle, *Platypus quercivorus*, die, and the factors affecting this mortality are still unknown. To examine this issue, the survival of all stems of fagaceous trees attacked by the ambrosia beetle was investigated in a secondary forest from 2008 to 2010. In an area of 93 ha, 2130 stems (1278 genets) of fagaceous trees were attacked by *P. quercivorus* during the study period, and 813 of these stems died. A generalized additive mixed model was constructed to predict the probability of mortality of the attacked stems. A best-fit model showed that the probability of mortality was higher in *Quercus crispula* than in *Castanea crenata*. A positive correlation was determined between the density of the attacked trees and the probability of mortality, suggesting that mass attack of *P. quercivorus* occurs not only on individual trees, but also on groups of trees. Assuming that trees attacked earlier in the season have a higher probability of mortality, the observed negative effects of altitude suggest that *P. quercivorus* initially seeks hosts at lower elevations.

51 **Introduction**

52

53           In general, the search pattern of animals consists of 2 parts. Firstly, when  
54 animals search a wide area without any resource cues, they move in a relatively straight  
55 path without turning (ranging). Secondly, after they detect resources, they scour a  
56 local area (local search), and then repeat their ranging and local search until they reach  
57 or gather the necessary resources (Jander 1975). This search pattern is also followed  
58 by ambrosia and bark beetles, with tree selection usually consisting of multiple  
59 phases—detection of host trees, evaluation of tree suitability, and acceptance of the host  
60 (Schoonhoven et al. 2005). Visual, olfactory, mechanosensory, and gustatory cues are  
61 considered to be involved in each phase.

62           Cues that ambrosia and bark beetles use to locate host trees can be predicted  
63 from differences in characteristics between attacked and intact trees. These  
64 differences have been determined in *Pinus* trees attacked by *Dendroctonus ponderosae*  
65 Hopkins (Coleoptera: Curculionidae) (Coops et al. 2006; Negrón et al. 2008; Negrón  
66 and Popp 2004; Olsen et al. 1996; White et al. 2007), and the information can be used to  
67 assess risk (Coops et al. 2009; Robertson et al. 2008; Wulder et al. 2006; Wulder et al.  
68 2009). However, analysis of damaged and intact trees without considering the  
69 multiple phases of host selection by the beetle may lead to incorrect interpretation of the  
70 results, because the cues in each phase are different. For example, the chemical factors  
71 involved in each phase of host selection by the conifer bark beetle were presumed to be  
72 different (Zhang and Schlyter 2004). Even within the same phase, different  
73 mechanisms may occur. Two conflicting mechanisms for the first phase of host  
74 selection by *Dendroctonus* beetles have been proposed: (1) attraction to host volatiles



(Pureswaran and Borden 2005; Pureswaran et al. 2004); and (2) random landing on trees (Moeck et al. 1981; Wood 1982). This contradiction was explained by the difference in timing of these two behaviors within the first phase (Saint-Germain et al. 2007).

In Japan, the ambrosia beetle, *Platypus quercivorus* (Murayama) (Coleoptera: Platypodidae), causes Japanese oak wilt by transporting the pathogenic fungus *Raffaelea quercivora* Kubono et Shin-Ito (Ito et al. 1998; Kinuura and Kobayashi 2006; Kubono and Ito 2002; Saito et al. 2001). The disease has spread throughout Japan since the 1980s (Kobayashi and Ueda 2005). From June to October, adult males of *P. quercivorus* fly to their host trees and bore shallow holes in them. Adult females join the males and, after mating, the males and females make galleries in the sapwood and deposit eggs at the terminal parts of these galleries. Hatched larvae feed on fungi that have been transported from old host trees by adult females. The larvae grow into the 5th larval stage by winter, and then enter hibernation. Pupation starts in spring, and new adults emerge starting in June (Soné et al. 1998).

Infection by *P. quercivorus* occurs in 3 successive phases—initial attack (Fig. 1a–b), mass attack (Fig. 1b–c), and cessation of attack. During the initial attack phase, some male beetles find a host tree, excavate a hole in the bark, and use an aggregation pheromone to attract their conspecifics (Tokoro et al. 2007). During the mass attack phase, aggregated beetles attack the host tree *en masse*, and cause death. It has been suggested that the attractiveness of trees bored by male beetles decreases after mating of the beetles, and this leads to the cessation of attack (Ueda and Kobayashi 2001).

Some trees survive the initial attack without receiving a mass attack, while other trees die because of the mass attack induced by the aggregation pheromone. In

the case of *Quercus crispula* Blume, the mortality of attacked trees was about 40% (Kamata et al. 2002). It is interesting to speculate under which situations the attack status of trees shifts from initial attack to mass attack. Factors that could affect the attack sequence include tree species, tree size, local environment, and timing of the attack.

It has been suggested that *P. quercivorus* can discriminate between tree species (Yamasaki and Futai 2012) with different susceptibilities (Kobayashi et al. 2004); therefore, a difference in the probability of initiation of a mass attack may be observed among tree species. The preference of *P. quercivorus* for targeting trees with wider trunks (Akaishi et al. 2006; Yamasaki and Sakimoto 2009) may be explained by the requirement of the species for large volumes of sapwood to construct galleries (Hijii et al. 1991). A similar preference might also be observed in the initiation of a mass attack.

*Platypus quercivorus* shows positive phototaxis (Igeta et al. 2003), and therefore the host selection behavior of the beetle may depend on forest light environments, which change temporally and spatially. Moreover, trees at different topographies are subjected to varying levels of drought stress (Eckhardt and Menard 2008; Guarín and Taylor 2005), and this might affect the probability of their death after attack. The initiation of a mass attack might also be affected by the density of the attacked trees (DEA). A high DEA could expose surrounding trees to high levels of aggregation pheromone, and result in a high probability of a mass attack. In addition, at sites where the attack by *P. quercivorus* begins early in the season, trees will be exposed to the attack for a longer period, which might increase their mortality risk.

In the present study, we investigated the factors affecting the initiation of a mass attack by *P. quercivorus*. We analyzed the survival data of attacked fagaceous trees collected from a 93-ha area, surveyed over 3 years. Among the proposed factors, the timing of the attack was impossible to measure throughout the wide area. Therefore, based on our results, we discuss the indirect effect of topography related to the timing of the attack.

## Material and methods

### *Study site and search for infected trees*

The present study was conducted in a secondary forest near the Hacchodaira bog, located in eastern Kyoto Prefecture, Japan (35°14' N, 135°50' E, Fig. 2a). The altitude of the study area ranged from 800 m to 970 m above sea level. The forest is in a cool-temperate forest zone, and is dominated by *Q. crispula* and *Castanea crenata* Sieb. et Zucc., which are highly susceptible and weakly susceptible, respectively, to Japanese oak wilt.

Damage caused by *P. quercivorus* in the study area was first observed in 2008. The 93-ha area was thoroughly searched from April to June in 2009, 2010, and 2011, to identify fagaceous trees that had been attacked by *P. quercivorus* in the previous year. The search effort was approximately 0.5 ha/h per person. Attacks by *P. quercivorus* were identified by the presence of holes bored by the beetle, and frass accumulation at the base of the tree. We identified the tree species and measured the diameter of each attacked tree at 130 cm above the ground (diameter at breast height [DBH]). The

survival of each attacked tree was determined and recorded, by checking the leaf flush of the investigated year. For multi-stemmed trees, DBH and survival were recorded for each individual stem. Differences in the mortality rate among trees species were tested using a 2-sample test for equality of proportions.

The location of each attacked tree was mapped using a global positioning system (GPS; GPS map 60 CSx, Garmin International, Inc., Olathe, Kansas). The longitude and latitude of each tree were projected onto a Transverse Mercator coordinate system in meter units. The altitude, topographic wetness index, and slope aspect of each location were calculated from a digital elevation model provided by the Geospatial Information Authority of Japan. The topography projection and calculation were performed using GRASS geographic information system (GIS) software (GRASS Development Team 2010).

#### *Preparation of explanatory variables*

Although it was presumed that the DEA affected the probability of mortality of an individual tree, the scale of this was unclear. Therefore, we prepared the basal area of attacked fagaceous trees (BA) by generating buffers around each stem, using 10 different scales ranging from a 2.5-m to a 25-m radius at 2.5-m intervals, and summing the BA of stems included in each buffer. When the generated buffer crossed the boundary of the study area, the BA was corrected by dividing the cumulative basal area, by the proportion of the buffer area inside the study area to the total buffer area.

We mapped the locations of attacked fagaceous trees (gray and black trees in Fig. 1c) in the study area, and calculated the surrounding BA of each attacked tree as a

candidate explanatory variable for predicting its mortality. The locations of intact fagaceous trees (trees drawn with dotted lines in Fig. 1c) were not mapped; therefore, the density of fagaceous trees, including intact and attacked trees (density of probable host trees [DEP]), could not be calculated. As a substitute for DEP, we prepared the categorical variable of vegetation type at the location of each attacked tree. Vegetation type was determined using the vegetation map created by the national survey on the natural environment, conducted by the Biodiversity Center of Japan, Ministry of the Environment. Five types of vegetation were observed in the study area—(1) secondary forest dominated by *C. crenata* and *Q. crispula*, (2) secondary forest dominated by Japanese cedar (*Cryptomeria japonica*) and *Q. crispula*, (3) secondary forest dominated by *F. crenata* and *Q. crispula*, (4) bog, and (5) grassland. Fagaceous trees were not observed in the grasslands.

The candidate explanatory variables for predicting the probability of mortality of trees attacked in the present year did not include the distance from trees attacked in the previous year, because of the lack of information regarding attacked trees outside the study area, and the prevention control of beetle emergence conducted in the study area. In the study area, diameter measurements of the trees have been recorded at 3-year intervals since 1980, in 13 fixed plots (boxes in Fig. 2b). No damage caused by *P. quercivorus* was observed in these plots or their surroundings, until the 10th measurements were conducted in 2007. In 2008, trees killed by *P. quercivorus* were first observed in the surrounding plot; therefore, nearly all the damage in 2008 was thought to be caused by beetles from outside the study area. It was difficult to check the locations of trees outside the study area that had been attacked in the previous year, i.e., 2007. In addition, irrespective of the present study, damage control trials were

conducted in the study area by Kyoto City, a conservator of this area. From May to July in 2009 and 2010, the basal parts of trunks of all dead trees attacked in the previous year were covered by vinyl sheets, up to 3 m or 4 m above the ground, to prevent beetle emergence and minimize damage to other trees. Therefore, it was difficult to evaluate the potential of trees attacked in the previous year to be sources of infection.

#### *Model construction and selection*

We modeled the probability of mortality of trees attacked by *P. quercivorus* by using a generalized additive mixed model (GAMM) with the package *gamm4* in R 2.15.3 (R Core Team 2013). The response variable used in the model was the survival of stems (0 for surviving stems and 1 for dead stems). The response variable follows a binomial distribution, and therefore we set the link function of the model as a logit link. The candidate explanatory variables were tree species, DBH, BA within a 2.5–25-m radius, altitude, topographic wetness index, slope aspect, and vegetation type. We assumed a nonlinear effect of slope aspect, and used a cyclic cubic regression spline as a smoother, to ensure that the values of the smoother at each end of slope aspect—0° and 360°—were the same.

The data for analysis were prepared at the individual stem level. We observed a high frequency of multi-stemmed fagaceous trees in the study area; further, stems of the same genet (individual tree) were basally connected with each other, implying a dependent structure. Therefore, the genet of trees, nested within tree species, was included in the model as a random intercept (Zuur et al. 2009). Model selection was performed in 2 steps, to obtain the best-fit model for predicting the

probability of mortality of trees attacked by *P. quercivorus*. In the first step, the best scale to calculate the density of attacked trees as an explanatory variable in the model for predicting the probability of mortality was evaluated. In the second step, the best-fit model with the lowest Akaike's information criterion (AIC) was selected from various combinations of candidate explanatory variables.

In the first step, 10 models were constructed—including the BA values at 10 different scales and all other candidate explanatory variables— and the model with the lowest AIC was selected as the full model. In the second step, the best-fit model was selected from the full model, by comparing the AIC of all candidate models with various combinations of explanatory variables. We used 7 candidate explanatory variables (tree species, DBH, BA, altitude, topographic wetness index, slope aspect, and vegetation type), and therefore the inclusion or exclusion of each variable resulted in 128 combinations. Among these 128 models, the model with the lowest AIC was selected as the best-fit model. The relative variable importance (RVI) of each candidate explanatory variable was calculated using the Akaike weights of the 128 models. Comparisons of AIC and calculation of RVI were performed using the *MuMIn* package in R.

## Results

In the study area, *P. quercivorus* attacks were observed on 3 fagaceous species, namely, *Q. crispula*, *Q. serrata* Murray, and *C. crenata*. In 2008, 2009, and 2010, we recorded 366 (227), 531 (320), and 1,233 (731) stems (numbers within parentheses are the number of genets), respectively (Table 1). In general, the mortality

rate of the attacked stems was higher in *Q. crispula* than in *C. crenata* (Table 1), and these differences were significant for all 3 years (2-sample test for equality of proportions: Chi-squared = 4.368,  $P = 0.037$  for 2008; Chi-squared = 24.328,  $P < 0.001$  for 2009; Chi-squared = 25.4,  $P < 0.001$  for 2010). The study forest was dominated by *Q. crispula* and *C. crenata*; the density of *Q. serrata* was low. In comparison with *Q. crispula* and *C. crenata*, *Q. serrata* showed a much lower number of attacked stems (Table 1); therefore, data on *Q. serrata* were excluded from the statistical analyses. In 2010, 40 stems of *Q. crispula* with a previous infection history (20 stems attacked in 2008 and 20 stems attacked in 2009) were reattacked by *P. quercivorus*. Data on these 40 stems were also excluded from the statistical analyses, because trees with a previous infection history are known to be resistant to *P. quercivorus* (Soné et al. 1998; Urano 2000). Thus, data on the remaining 2063 stems were used for the statistical analyses.

The annual distribution of attacked *Q. crispula* in the study area differed from that of *C. crenata* (Fig. 3). Clumps of attacked *Q. crispula* were observed at the lower edges of the ridge face on the bog (Fig. 3). Generally, the density of attacked *Q. crispula* was low on the west side of the study area (Fig. 3), where the vegetation was dominated by Japanese cedar and *Q. crispula* (Fig. 2b). Similar to this area, the center area (bog) was distinguished by a low density of attacked *Q. crispula* (Fig. 3). In 2008, attacked *C. crenata* trees were distributed only on the north side; however, after 2009, their distribution range extended to the south (Fig. 3).

We compared the ability of 10 models to predict the probability of mortality of the attacked trees, by using tree species, DBH, altitude, topographic wetness index, slope aspect, vegetation type, and BAs calculated at 10 different scales as explanatory variables (Fig. 4). The AIC of the model decreased with an increase in the radius of



the area used to calculate the BA, reaching its lowest value at a 15-m radius; thereafter, the AIC increased (Fig. 4). Therefore, the BA within a 15-m radius was used as a candidate explanatory variable for modeling the probability of mortality of the attacked trees.

DBH, topographic wetness index, slope aspect, and vegetation type were not selected as explanatory variables in the best-fit model to predict the probability of mortality of the attacked trees. When *C. crenata* was set as a baseline, the estimated coefficient for *Q. crispula* was positive (tree species in Table 2). The estimated coefficient for the BA was also positive, indicating that this variable had significant positive effects on the probability of mortality of the attacked trees (Table 2). A significant negative effect on the probability of mortality was detected for altitude (Table 2). Tree species, BA, and altitude were equally important predictors in the model (RVI = 0.99 or 1.00, Table 2). Among the variables not selected for the best-fit model, DBH showed the highest RVI (0.51), while vegetation type showed the lowest RVI (0.16).

## Discussion

In the present study, we showed that the mortality of trees attacked by *P. quercivorus* was significantly higher in *Q. crispula* than in *C. crenata* (Table 1); further, tree species was included in a best-fit model to predict the probability of mortality (Table 2), implying that the probability of mortality was higher in *Q. crispula* than in *C. crenata*. *Quercus crispula* is a more suitable host for *P. quercivorus* than is *C. crenata* (Tarno et al. 2011); therefore, the beetle is more inclined to use *Q. crispula* as an attack

290 target (Yamasaki and Futai 2012), resulting in a higher probability of death for this  
291 species.

292 We demonstrated a positive effect of DEA on the probability of mortality  
293 (Table 2), suggesting that mortality is low when the tree is individually attacked (i.e.,  
294 with a low density of surrounding attacked trees), and high when the tree is attacked  
295 together with surrounding individuals (i.e., with a high density of surrounding attacked  
296 trees). In other words, changes in infection phases, from initial attack to mass attack  
297 (and subsequent death of the attacked tree), tend to occur when groups of trees are  
298 attacked. Therefore, it is likely that mass attacks of *P. quercivorus* occur not only in  
299 individual trees, but also in groups of trees. The ambrosia and bark beetles are thought  
300 to attack trees *en masse* to break down the host tree's resistance; further, the male  
301 beetles use an aggregation pheromone to attract conspecifics to an individual tree  
302 (Wood 1982). When attacked trees are clumped together (Fig. 3), the effects of the  
303 aggregation pheromone might also work on a larger scale, and the beetle might be  
304 attracted primarily to a group of trees. The BAs calculated at a 15-m-radius scale, i.e.,  
305 706.5 m<sup>2</sup> in area, were good predictors of the probability of mortality of the attacked  
306 trees (Fig. 4), and may show the effective scale of clumped attacked trees as attractants  
307 to the beetle. In the case of initial attack by *P. quercivorus*, the effective DEP scale  
308 was 900 m<sup>2</sup> (Yamasaki and Sakimoto 2009), which is slightly higher than the scale  
309 suggested in the present study. Beetles might begin to search for a suitable host tree  
310 within a wide range, and after detecting clumped host trees, might narrow the target,  
311 and precipitate a mass attack.

312 Previous studies showed negative effects of altitude on the probability of  
313 mortality of ponderosa pine caused by *Ips* beetles (Negrón et al. 2009). These

negative effects were explained by the shorter growing season for the beetles, caused by the cooler temperatures at higher altitude (Williams et al. 2008). A similar negative effect of altitude was determined in the present study (Table 2); however, considering the small range of altitude (800–970 m) in the study area, it is improbable that the length of the beetle's growing season differs among trees at different altitude. The decrease in the probability of mortality of the attacked trees with an increase in altitude may have arisen because of the host-seeking process of *P. quercivorus* in forests. A previous study showed that *P. quercivorus* moves upward along slopes (Esaki et al. 2004). *Platypus quercivorus* might initially seek hosts at lower elevations in a forest, and trees at the lower elevations might have a higher probability of mortality because of their longer exposure to the beetle.

As reviewed in Fettig et al. (2007), insect resistance mechanisms are damaged in trees that are stressed by factors such as drought, and this causes high susceptibility to attack by the bark beetle. Moreover, under severe drought conditions, susceptibility to beetle attack is further increased by other stress factors (Eatough Jones et al. 2004). In the present study, we determined no effect of wetness on the mortality of the attacked trees (the topographic wetness index was not selected in the best-fit model, Table 2). Vegetation type was also not selected in the best-fit model (Table 2). The model confirmed the lack of a relationship between water availability and the mortality of the attacked trees. The dataset for the present study included 4 vegetation types, namely, bog and 3 types of secondary forest. Water availability was evidently higher for trees growing in a bog than for trees growing with other vegetation types; however, the mortality of the attacked trees did not differ among vegetation types. The mortality of trees attacked by *P. quercivorus* is considered to be mainly affected by the occurrence

of mass attacks, and the local environment of trees may have little effect once a mass attack is initiated.

*Platypus quercivorus* shows positive phototaxis, and might concentrate in stands with more light (Igeta et al. 2003). A study conducted at Hacchodaira—the same site as that used in the present study—showed a negative effect of DEP at a large scale on the probability of beetle attack (Yamasaki et al. in press), suggesting a beetle preference for bright stands with low DEP. Assuming that phototaxy functions during the host-seeking process, the heterogeneity of light environments in a forest interior caused by differences in slope aspect might have some effects on beetle aggregation. However, in the present study, the mortality of attacked trees was not affected by slope aspect (Table 2). Therefore, positive phototaxis may function at an earlier time, such as immediately after beetle emergence from holes, in order to orient them toward the sky. Nevertheless, many uncertainties regarding the flight behavior and flight height of *P. quercivorus* exist.

Assuming that the DEP was uniform within the area of the same vegetation type, exclusion of vegetation type (which showed the lowest RVI; Table 2) from the model indicated no difference in mortality among attacked trees with different DEP values. However, even for the same vegetation types, DEP differed at a local scale. Therefore, the possibility that DEP affects the mortality of attacked trees cannot be excluded. The inclusion of DEP at various scales as a candidate explanatory variable for the model may clarify this issue. Moreover, to elucidate a more precise host selection process of *P. quercivorus*, the inclusion of variables not measured in the present study (for example, the distance from trees attacked in the previous year) as candidate explanatory variables is required.

## Conclusion

Previous studies on trees attacked by *P. quercivorus* have considered all probable host trees in a certain area as subjects of analysis, and have shown the preferences of the beetles during their attack process with regard to species (Yamasaki and Futai 2012), size (Akaishi et al. 2006; Yamasaki and Sakimoto 2009), and infection history (Yamasaki and Futai 2008). However, the attack process of the beetles is thought to be divided into 2 phases—the initial attack and the mass attack (Fig. 1). In the present study, by analyzing only attacked trees, we clarified the factors affecting the initiation of mass attack. The exclusion of DBH and vegetation type from the best-fit model for predicting the probability of mortality of the attacked trees suggests that *P. quercivorus* selects clumped, wide trees not as a mass attack target, but as an initial attack target. The inclusion of BA in the best-fit model showed that *P. quercivorus* selects dense stands of attacked trees as mass attack targets. The results of a 3-year survey of beetle infection over wide areas revealed the detailed host selection process of the ambrosia beetle, *P. quercivorus*.

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**Table 1** Mortality rate of stems attacked by *Platypus quercivorus*, and number of attacked stems (within parentheses), in a secondary forest near the Hacchodaira bog, located in eastern Kyoto Prefecture, Japan. Data are separately shown for 3 fagaceous species, in 2008, 2009, and 2010. In all 3 years, the mortality rate was significantly higher in *Q. crispula* than in *C. crenata* (2-sample test for equality of proportions: Chi-squared = 4.368,  $P = 0.037$  for 2008; Chi-squared = 24.328,  $P < 0.001$  for 2009; Chi-squared = 25.4,  $P < 0.001$  for 2010).

	2008	2009	2010
<i>Quercus crispula</i>	40.3% (325)	45.5% (453)	39.5% (1124)
<i>Quercus serrata</i>	50.0% (2)	0% (8)	0% (17)
<i>Castanea crenata</i>	23.1% (39)	14.3% (70)	13.0% (92)

**Table 2** Estimated coefficients, their standard errors, and  $z$ -statistics of variables selected for a best-fit model ( $n = 2063$ , AIC = 2196.764) to predict the probability of mortality of fagaceous trees caused by the ambrosia beetle, *Platypus quercivorus*, in a secondary forest near the Hacchodaira bog, located in eastern Kyoto Prefecture, Japan.

Variable	Estimate <sup>a</sup>	SE	$z$	$P^b$	RVI <sup>c</sup>
Tree species <sup>d</sup>	3.85180	1.05806	3.640	0.00027 ***	1.00
BA <sup>e</sup>	4.03259	0.73263	5.504	<0.00001 ***	1.00
Altitude	-0.02997	0.00904	-3.316	0.00091 ***	0.99
DBH <sup>f</sup>	-	-	-	-	0.51
Topographic wetness index	-	-	-	-	0.39
Slope aspect	-	-	-	-	0.39
Vegetation type	-	-	-	-	0.16

<sup>a</sup>Variables without estimates were not selected as explanatory variables for a best-fit model

<sup>b</sup>Significant differences from zero were tested using  $z$ -statistics (\*\* $P < 0.01$ , \*\*\* $P < 0.001$ )

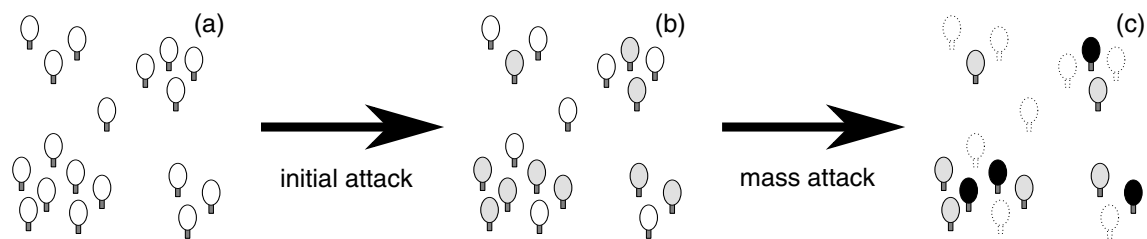
<sup>c</sup>RVI = relative variable importance, calculated using Akaike weights of all candidate models

<sup>d</sup>Tree species = species of attacked tree (estimated intercept for *Quercus crispula*, when *Castanea crenata* is set as a baseline, is shown)

<sup>e</sup>BA = basal area of attacked fagaceous trees within a 15-m radius

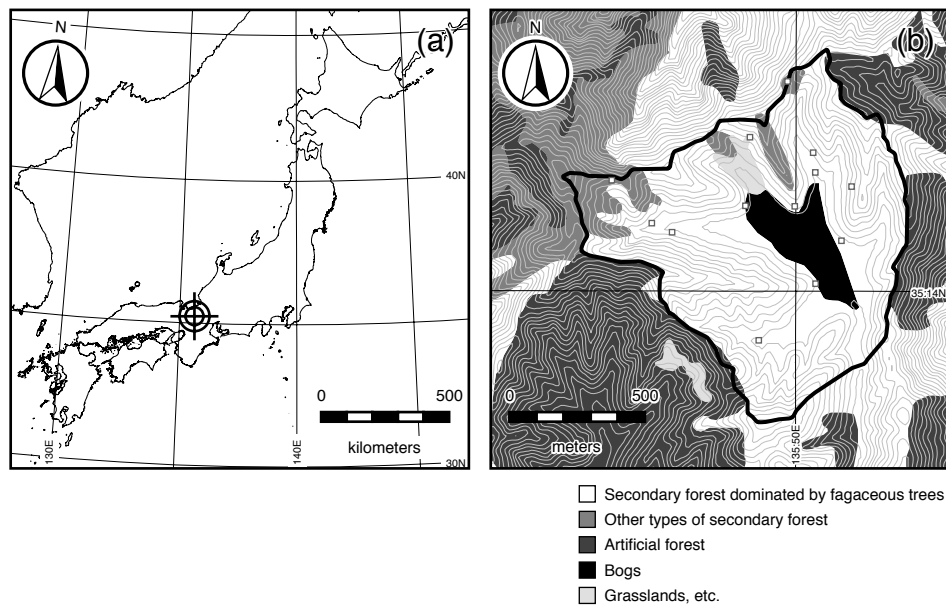
<sup>f</sup>DBH = diameter at breast height, i.e., diameter of the attacked tree at 130 cm above ground

**Fig. 1** Course of infection by *Platypus quercivorus*. (a) Intact fagaceous trees distributed in a forest. (b) Some trees receive an initial attack by the beetle. (c) Mass attack occurs on some of the trees that received the initial attack. White, gray, and black trees show intact trees, trees that received an initial attack, and trees that received a mass attack subsequent to the initial attack, respectively. Trees drawn with a dotted line are not a target of the mass attack.

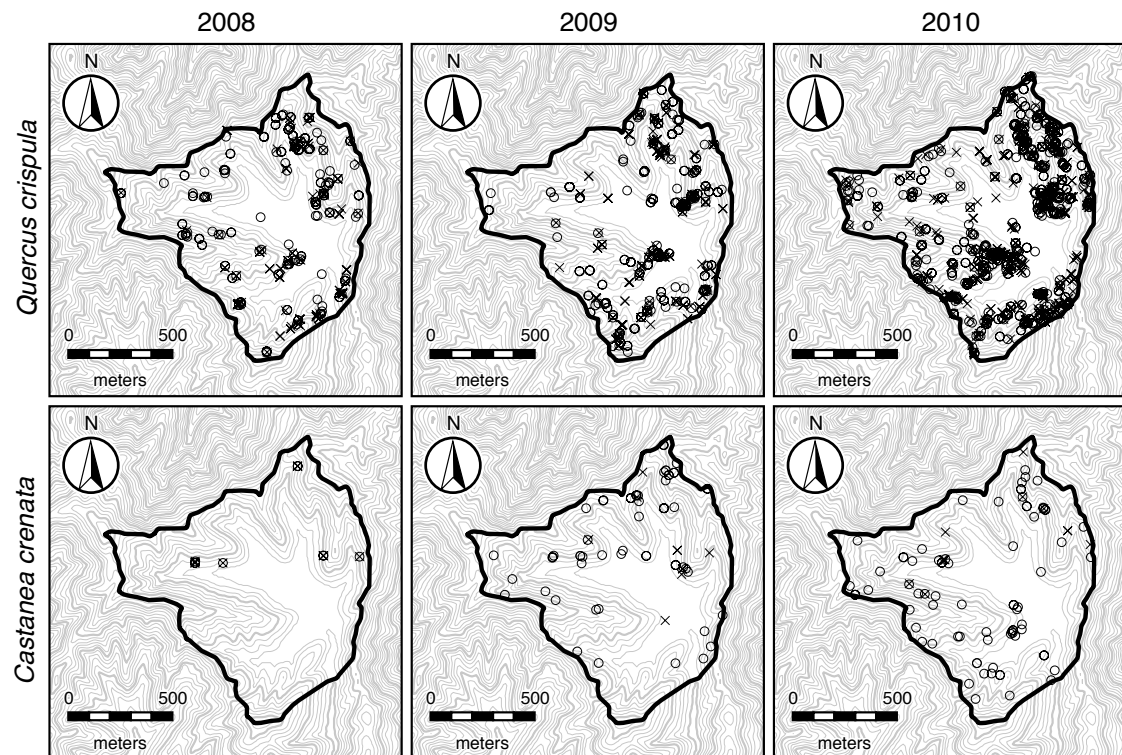




**Fig. 2** (a) Location of the study site in Japan. (b) Vegetation type in and around the study area. The thick line shows the study area. The white, gray, dark gray, black, and light gray areas show the secondary forest dominated by *Castanea crenata* and *Quercus crispula*, other types of secondary forest, artificial forest, bogs, and other types of vegetation such as grasslands, respectively. Gray lines show contour lines at 10-m intervals. Boxes show the location of 13 fixed plots set up in 1980.



**Fig. 3** Distribution of *Quercus crispula* (top) and *Castanea crenata* (bottom) attacked by *Platypus quercivorus* in 2008 (left), 2009 (center), and 2010 (right) in a secondary forest near the Hacchodaira bog, located in eastern Kyoto Prefecture, Japan. Circle, surviving tree; cross, dead tree.



**Fig. 4** Akaike's information criterion (AIC) of 10 different models to predict the mortality probability of fagaceous trees attacked by *Platypus quercivorus* in a secondary forest near the Hacchodaira bog, located in eastern Kyoto Prefecture, Japan. The basal areas of attacked trees calculated within a radius of 2.5–25 m of the target tree were included in each model, together with the other candidate explanatory variables.

